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Genetic gain in perennial ryegrass (*Lolium perenne*) varieties 1973 to 2013

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Abstract Perennial ryegrass (*Lolium perenne)* forms the basis of grassland production in temperate pastures and is globally one of the most important forage grasses. Consequently, there has been large plant breeding industry investment over the past 40 years in producing new varieties and independent testing systems designed to identify and list those with the most improved performances. This study was conducted at the Plant Testing Station, Crossnacreevy, Northern Ireland and compared the DM yield and sward density of new varieties submitted from 1973 to 2013 and grass digestibility from 1980 to 2013, under conservation and simulated grazing managements. A variety × years matrix was compiled for each parameter and comparable means between varieties never in side by side performance trials were produced. Dry matter yields showed an overall significant ($p < 0.001$) average annual increase of 0.52 % under conservation and 0.35 % under simulated grazing, with similar gain levels within maturity groups or ploidies. These rates were not constant over time, and periods of no gain occurred in various variety groupings. Sward density of the examined varieties did not change significantly. Herbage digestibility showed no improvement over the timeframe but had the largest differences between concurrent varieties, indicating that improvements were possible in the future. The study indicated that plant breeding gains were primarily DM yield focused with sward density remaining stagnant over the 40 years, while the lack of grass digestibility improvement appeared to only require more time to overcome. Evidence of benefits and risks of variety testing influences on plant breeding objectives was discussed.

Keywords Breeding · Genetic gain · Recommended lists · Ryegrass · Varieties

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Introduction

Perennial ryegrass is the most widely used forage species for ruminant production systems in cool-temperate agricultural regions like Ireland and the UK. Grassland accounts for 76 % of the total agricultural area in Ireland (CSO 2012) and 69 % in the UK (FAO 2008). Consistent use of perennial ryegrass varieties in ruminant grazing production systems can be attributed to high DM productivity potential, high forage digestibility throughout the grazing season and the large varietal diversity adapted to a range of growing conditions and farming practices. Limitations to land availability coupled with increasing environmental requirements to reduce greenhouse gas emissions and N losses to ground water are placing increased pressure on grass based animal production systems to provide additional quantities of high quality forage. The ability of farmers to increase forage yield, through increased fertiliser inputs is limited (Parsons et al. 2011). Thus, increased performance must be achieved by other means and one of the most important avenues is grass breeding.

Forage grass breeding began much more recently compared to most other major agricultural species. Only at the beginning of the 20th century did grass varieties begin to emerge with good agronomic performances (Wilkins and Humphreys 2003) with perennial ryegrass breeding being primarily focused on yield and persistence since the 1970s. Although total DM yield remains a key objective within forage ryegrass breeding, there is increased emphasis on seasonal DM production, quality and sward density. A further key objective is to develop varieties which are more productive and persistent under grazing (Evans and Williams 1987), rather than a higher average performance under both grazing and silage production. Since the 1980s onwards, increased digestibility has been given greater importance in testing programmes. The slow inclusion of other forage quality traits in variety testing across Europe has delayed gains in nutritional value as breeding priority was originally for DM production and persistence to enter recommended list (RL) markets. If these changes in breeding emphasis are to be delivered at farm level, the authorities that test and register new varieties may need to also change the emphasis placed on the criteria within testing programmes.

Following the introduction of the official testing scheme in Northern Ireland (NI) and the first publication of RLs in 1973, the ryegrass seed sown on farms in NI has predominantly been comprised of varieties that were currently recommended by the Department of Agriculture (currently Department of Agriculture and Rural Development, DARD), (Gilliland et al. 2007). Despite this production of proven superior varieties, reseeding activity has been in a decline over a long number of decades (Grogan and Gilliland 2010). To some extent, the reduction in reseeding activity may reflect improvements in variety persistency as proposed by Gilliland et al. (2007), which would have increased the productive lifetime of swards. Gilliland et al. (2007) reported that the decline in reseeding from 1980 to 2004 in NI was not progressive as large dips occurred during cattle disease outbreaks and following reduced government subsidies. The implication was that farmers were not regarding the improvements in new varieties as sufficiently valuable to justify reseeding costs when farm budgets came under pressure. So providing a definitive measure of genetic gain in varieties could help promote best practice by encouraging the replacement of older, poor performing pastures.

The rate of genetic gain achieved through grass breeding has never been extensively studied before under Irish conditions. A complicating factor is that genetic gain is specific to the growing conditions and management practices imposed. Therefore, varieties can re-rank when managed under different conditions (Wilkins 1989; Wims et al. 2009) and hence Wilkins and Humphreys (2003) reported large regional variations in genetic gains from forage grass breeding. For example, they reported genetic gains of 4–5 % in DM yield per decade achieved in North-Western Europe with similar gains reported in New Zealand compared with 0–1% per decade in the USA in the important forage grasses. This variation is largely due to differences in climatic stress factors and different disease and pest pressures. In NI, the mild damp climate with low disease incidences and few grass pests provides ideal conditions under which ryegrass can express its full genetic potential for herbage DM production (Camlin 1997).

The management protocol for the official RL testing programme in NI has employed a standardised simulated grazing and conservation management since the 1970s and has always been conducted at the same site. This provides a unique dataset of variety performances generated under low stress conditions (low disease levels, mild winters, warm moist summers and free of any genotype × site interaction. The objective of this study was therefore to produce an accurate estimation of the genetic progress achieved in perennial ryegrass breeding over the last four decades. This was achieved by using the annual performance data compiled from applicant varieties that were subsequently listed on the Northern Ireland RL of

Grass and Clover varieties, between 1973 and 2013. Three performance parameters were assessed (DM yield, sward density and digestibility) under conservation and simulated grazing and differences between ploidy and maturity groupings were also examined.

Materials and methods

Variety testing and data accumulation

The data were compiled from the Value of Cultivation and Use trials conducted at the Crossnacreevy Plant Testing Station, Co. Down (54°32′N, 5°52′W) on a medium loam soil, for the period of 1973–2013. These data were primarily used to compile the NI recommended variety lists and comprised of 202 perennial ryegrass varieties of which 20 % were early maturing, 43 % were intermediate and 37 % late maturing types (Table 1). These varieties were included in every recommended variety list since 1973.

The production potential of the varieties were tested under a simulated grazing management in the second full harvest year after sowing and for conservation production in the second harvest year until 1985 and in the third year thereafter. This was because, initially two separately sown plot trials were used to assess performance under the two management regimes in two growing seasons, but were then combined into a single sowing conducted over three harvest years. The combined trial scheme involved grazing with a beef suckler herd in the first full growing season, followed by yield assessment under a simulated grazing in the second year and conservation in the final third year of the trial. The basic methodology used in the two yield managements was unchanged since the first trials in the 1970s.

Table 1 Number of varieties examined in each maturity and ploidy combination

Maturity		Totals
Early		
Diploid	22	
Tetraploid	18	40
Intermediate		
Diploid	50	
Tetraploid	37	87
Late		
Diploid	44	
Tetraploid	31	75
Overall total		202

A sequential annual sowing of successful candidate varieties was conducted to initially produce five simulated grazing and five conservation harvest years over a seven year period (Table 2). Thereafter, varieties were normally sown only on alternative years to eventually provide a minimum of five trial years of data within any decade that the variety was recommended. Once the variety was outclassed on the RL it was not re-sown. Over the 44 year period of assessment (Harvest years 1970–2013), no recommended variety was present in every harvest year and many varieties were never sown in the same trial, which produced an incomplete data matrix. Also included in every trial was a number of control varieties, which unlike the candidates, were sown in a continuous series of consecutive years. When a control variety was replaced a period of overlap was carried out when both the new and old controls were sown in the same trial. This provided an unbroken sequence of control varieties from 1970 to 2013, which made it possible to produce a statistical comparison between candidate varieties that were sown and tested several decades apart.

The annual test procedures imposed under the two yield management regimes were performed as described by FERA (2014). The simulated grazing management comprised seven DM yield harvests ranging from early March to early November to a residual height of 3 cm with 320 kg N/ha/annum. Dry matter yield was measured at every cut and digestibility was measured on the August defoliation when all varieties should have resumed vegetative growth. The conservation management comprised of five DM yield harvests, cut to a residual height of 6 cm with 350 kg N/ha/annum. The first conservation cut was taken at the 67D stage followed by a second cut six weeks later and then on a monthly defoliation cycle to simulate back end grazing. All final harvests were normally completed by the end of October each year. Dry matter digestibility was sampled at the first two silage cuts using 100 g subsamples and analyses as described by FERA (2014).

Sward density was measured at the end of the simulated grazing season, estimated by visual assessment using a 0–9 score in the autumn on each

Table 2 Testing schedule for new candidate varieties over a seven year period

Evaluation cycle of trials (years)							
0	1	2	3	4	5	6	7
Sow I NL	(H1 C)	H2 SG	H3 C				
	Sow II NL	(H1 C)	H2 SG	H3 C			
		Sow III RL	Graze	H2 SG	H3 C		
			Sow IV RL	Graze	H2 SG	H3 C	
				Sow V RL	Graze	H2 SG	H3 C

Sow I–V Trial sowing series, *H1–3* Harvest years 1–3*, *NL* National list, *RL* Recommended list, *C* Conservation management, *SG* Simulated grazing management, *Graze* Grazed with cattle, no recordings, *H1 C* Year 1 data not used in this study

* Before 1980 there were only 2 harvest years but separately sown trials for each management

simulated grazing trial. This score indicated the amount of ground cover or sward density of the sown ryegrass in the sward, ranging from zero to less than 10 % cover (score 0) up to 90–100 % cover (score 9).

The final data set comprised the total annual DM yield and sward density of the 202 varieties over the entire 41 years of recommended listing (1973–2013), but as some data entries were not available for some parameters the total variety numbers ranged between 197 and 202. Grass quality testing did not begin until 1980 and so digestibility data was only available for 116 varieties, over 34 years (1980–2013).

Statistical analysis

Four over-years data matrices were compiled, comprising the simulated grazing yields, conservation yields and sward density for 1973–2013 (inclusive) and for digestibility from 1980 to 2013 (inclusive). These incomplete varieties × years matrices were analysed using the fitted constant statistic defined by Yates (1933) and Silvey (1978) to provide comparable over-years' means for each recommended variety. This was despite not having all varieties in all trials in all years. These standardised variety mean values were regressed against the year of application (year of entry into testing) for diploid and tetraploid varieties and for maturity group (early, intermediate and late), to determine the rate of gain over time in these categories of perennial ryegrass. Regression models were fitted with the REG procedure on SAS (SAS 2011), to determine the significance of the performance range in each trait for each variety group by comparing the base year of application with the most recent data entries in 2013.

By assigning each variety to its year of application into trials, any progressive change in genetic gain was examined as new varieties were bred and listed and older ones were removed.

Results

Dry matter yield

When the individual variety DM yields were regressed against their year of application there was a progressive rising trend in overall DM yield across the 41 year period of 1973–2013 (Fig. 1). This upward trend was evident for both the conservation and simulated grazing managements though with a stronger association of DM yield increase to year of application for conservation ($r = 0.73$). This genetic gain in variety performance potential was highly significant ($p < 0.001$) in both managements (Table 3) but was numerically greater for conservation (+21.4 %) than for simulated grazing yield (+14.4 %). When the average yield of the recommended varieties within each decade was compared, there was a highly significant ($p < 0.001$) increase in DM yield. Rise in trends were not constant across each decade, however, as there were periods when no progress was achieved and periods of both positive and negative yield changes. This is clearly evident in the significant and non-significant positive/negative gain values in each of the four decades for both the simulated grazing and conservation yields (Table 4 'All Varieties'). Most notably in the 1990s total simulated grazing and conservation yields rose significantly but in the preceding 1980s they fell, though not significantly.

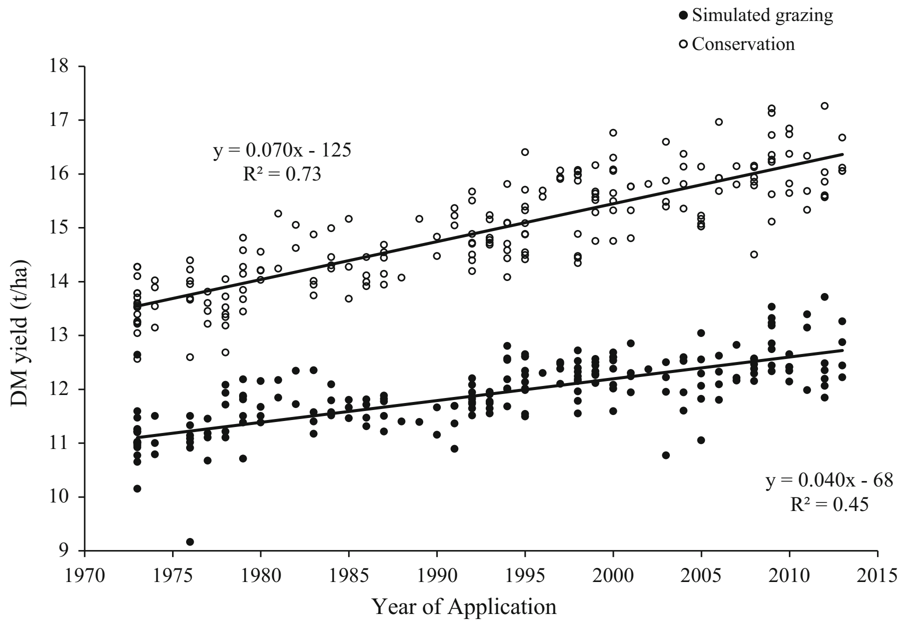

Fig. 1 Genetic gain in perennial ryegrass varieties under simulated grazing and conservation managements 1973–2013

Table 3 Genetic gain in DM yield of perennial ryegrass maturity groups 1973–2013

	Conservation					Simulated grazing				
	No. of varieties	Gain (%)	Change (t/ha)	SE	*p* value	No. of varieties	Gain (%)	Change (t/ha)	SE	p value
All varieties	199	+21.4	+2.8	0.003	< 0.001	202	+14.4	+1.6	0.003	< 0.001
Early	39	+19	+2.7	0.006	< 0.001	40	+17.9	+2.0	0.006	< 0.001
Intermediate	84	+22.6	+3.0	0.005	< 0.001	87	+10.5	+1.2	0.003	< 0.001
Late	76	+22.6	+2.8	0.004	< 0.001	75	+16.4	+1.8	0.005	< 0.001

When comparisons between the average yields of each annual RL were compared (data not shown) the same pattern was evident, as the average variety performance for either conservation or simulated grazing fell on some lists, within the overall annual rising trend. Nonetheless, the total increase in average variety yield between the RL in 1973 compared to 2013 was +2.8 t/ha DM for the conservation management (13.1 t/ha DM 1973–15.9 t/ha DM 2013) and +1.6 t/ha DM under simulated grazing (10.9 t/ha DM 1973–12.5 t/ha DM 2013). This represented an average annual percentage rise of 0.52 % in conservation and 0.35 % for simulated grazing.

When comparisons between the three maturity groups were carried out the fluctuating pattern of yield increase was again evident when regressed against application year (Fig. 2). The fluctuations evident in the overall comparison (Fig. 1) were, however, only expressed in the early and intermediate groups and most clearly in simulated grazing. These two groups rose and fell almost in synchrony but the late group appeared to have a more consistent progressive rise. Even so, it was clearly shown that in all three groups and under both managements there was a number of under and over performing varieties at certain time points and also that the emerging varieties were not always superior in yield to those that had entered the list in preceding years. Again, the overall significant ($p < 0.001$) increase in DM yield for each management was still present in each maturity group (Table 3), with the higher rate of increase consistently achieved under the conservation management. Furthermore, Table 4 shows that the significant and non-significant positive/negative gain values evident in all varieties analysis was also present in each of the three maturity groups. The significant gains in 1990s when

Table 4 Comparison of genetic gain in DM yield in four consecutive decades

	Simulated grazing					Conservation				Sward density			
	Decade	Gain (%)	Change (t/ha)	SE	*p* value	Gain (%)	Change (t/ha)	SE	*p* value	Gain (%)	Change ±	SE	*p* value
All varieties	1970s	+1.8	+0.2	0.05	NS	+2.2	+0.3	0.03	NS	−0.5	−0.3	0.05	NS
	1980s	−2.9	−0.4	0.02	NS	−0.7	−0.1	0.03	NS	+6.1	+3.3	0.11	0.05
	1990s	+4.8	+0.5	0.02	< 0.01	+6.9	+0.9	0.03	< 0.01	−7.0	−4.0	0.07	0.08
	2000s	+2.5	+0.3	0.02	NS	+3.3	+0.5	0.03	0.07	+0.6	+0.3	0.13	NS
Early	1970s	+2.7	+0.3	0.09	NS	+1.4	+0.2	0.06	NS	−4.2	−2.2	0.78	NS
	1980s	−6.0	−0.7	0.05	0.06	−1.4	−0.2	0.09	NS	+7.9	+4.4	0.94	NS
	1990s	+7.6	+0.9	0.03	< 0.05	+7.6	+1.1	0.04	< 0.01	−16	−9.5	0.51	< 0.05
	2000s	+5.7	+0.7	0.04	NS	+6.5	+1	0.07	NS	+5.4	+2.8	0.37	NS
Intermediate	1970s	+8.4	+1.0	0.04	< 0.05	+0.7	+0.1	0.06	NS	+6.6	+3.4	0.96	NS
	1980s	−5.7	−0.7	0.02	< 0.05	−3.4	−0.5	0.06	NS	+13.8	+7.1	0.53	NS
	1990s	+5.1	0.6	0.02	< 0.01	+5.4	+0.8	0.04	< 0.05	−3	−1.7	0.39	NS
	2000s	+6.7	0.8	0.05	NS	+6.6	+1	0.04	< 0.05	−7.9	−4.4	0.43	NS
Late	1970s	−2.7	−0.3	0.10	NS	+3.7	+0.5	0.03	< 0.05	+0.5	+0.3	0.68	NS
	1980s	−0.9	−0.1	0.02	NS	+2.1	+0.3	0.04	NS	+2.1	+1.2	0.38	NS
	1990s	+7.9	+0.9	0.02	< 0.01	+4.7	+0.7	0.05	NS	−5.7	−3.2	0.46	NS
	2000s	+1.6	+0.2	0.02	NS	−0.6	−0.1	0.03	NS	+3.4	+1.8	0.20	NS

all varieties were examined together was also still evident when the three maturity groups were analysed separately, with one exception for late conservation, when the positive gain was not significant (Table 4).

Segregating the data into diploid and tetraploid groups also showed that highly significant ($p < 0.001$) increases in DM yield had occurred across the study period under both managements (Table 5), and also that the gains were again largest for conservation use. Under simulated grazing the rate of gain in tetraploids ($p < 0.001$) was numerically greater than for diploids ($p < 0.001$) but under conservation percentage gains between tetraploids and diploids were closer (20.5 vs 19.4 %). When subdivided into maturity groups all differences and rankings remained largely unchanged and with high significances ($p < 0.001$).

Sward density

When the individual variety sward densities were regressed against application year, there was no evidence of any genetic gain across the entire study period (Fig. 3). Overall, the regression produced a small but insignificant decrease in sward density of −3.8 % from 1973 to 2013. This negative but non-significant trend was confirmed when the data was further interrogated to examine for differences between the maturity groups and between the two ploidies (Table 6). The only significant decline was in the late maturing group when ploidy was not separated. When the data was examined within decades (Table 4) periods of both positive and negative gain were found, though the only changes approaching significance were an increase in the 1980s with all maturities and ploidies grouped ($p < 0.05$), followed by a decline in the 1990s ($p = 0.08$) plus a significant ($p < 0.05$) decline for early maturing varieties in the 1990s. Among the non-significant responses it was noted that the intermediate varieties always recorded a positive gain value in both ploidies with early and late varieties alternating between positive and negative gains across both ploidies (Table 6).

Digestibility

Regressing the digestibility content of the varieties against year of application for the 34 year period of 1980–2013 revealed no evidence of a consistent improvement over time (Fig. 4). While the regression showed a slight but insignificant rising trend, the

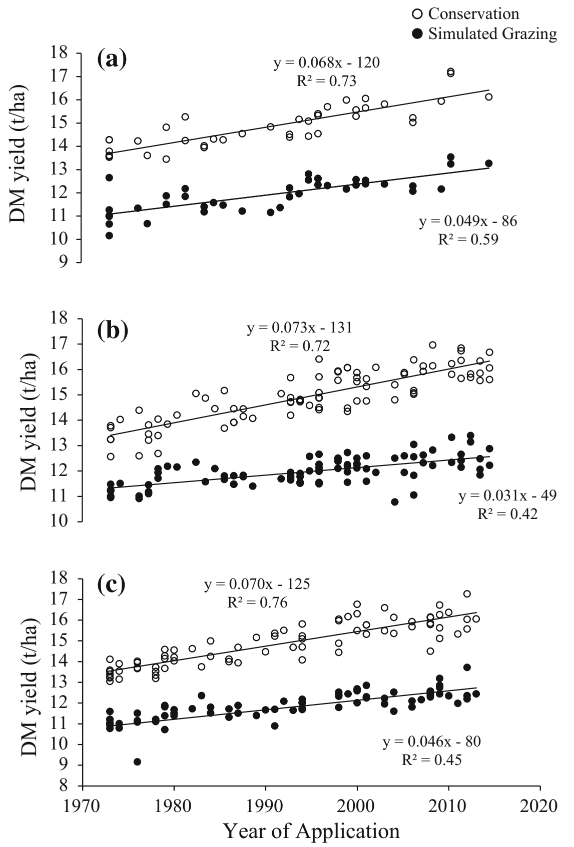

Fig. 2 Genetic gain in DM yield of perennial ryegrass varieties under simulated grazing and conservation managements 1973–2013, **a** Early-maturing varieties, **b** Intermediate-maturing varieties, **c** Late-maturing varieties

majority of varieties tested were in the later years of this period, where they largely formed an inconsistent cloud. This created the very weak association between digestibility and application year in both management systems. On further examination of the data (Table 7), this positive trend was evident in all maturity and ploidy groupings under both managements, but only under conservation when all varieties were grouped together was this rising trend close to reaching significance ($p < 0.07$). Overall, there was a general trend for a higher gain value under conservation (+2.5 %) than simulated grazing (+2.0 %), neither trend was significant. When all the sub-categories of maturity group and ploidy were compared the conservation gains were only numerically greater for early and intermediate varieties, were numerically lower for late and broadly the same for both diploids and tetraploids varieties. Ploidy was not further subdivided into maturity groups for digestibility due to the small numbers in some of these groups.

Discussion

Each standardised value, calculated by fitted constant analysis for each variety, was an over-years average relative to the actual performance of the control varieties that linked across the years. This meant that the individual performance value used for each variety within each maturity/ploidy/management category

Table 5 Genetic gain in DM yield of diploid and tetraploid perennial ryegrass varieties 1980 to 2013

	Diploid					Tetraploid				
	No. of varieties	Gain (%)	Change (t/ha)	SE	*p* value	No. of varieties	Gain (%)	Change (t/ha)	SE	*p* value
Conservation diploid tetraploid										
All varieties	115	+19.4	+2.6	0.003	< 0.001	84	+20.5	+2.7	0.003	< 0.001
Early	21	+18.4	+2.5	0.009	< 0.001	18	+18.1	+2.5	0.01	< 0.001
Intermediate	48	+22.0	+2.9	0.005	< 0.001	36	+17.9	+2.5	0.007	< 0.001
Late	46	+17.8	+2.4	0.004	< 0.001	30	+21	+2.9	0.006	< 0.001
Simulated grazing										
All varieties	117	+13.4	+1.5	0.004	< 0.001	85	+16.4	+1.8	0.004	< 0.001
Early	22	+17.3	+1.9	0.01	< 0.001	17	+19.4	+2.4	0.003	< 0.001
Intermediate	51	+9.7	+1.1	0.004	< 0.001	37	+12.3	+1.4	0.006	< 0.001
Late	44	+14.5	+1.6	0.008	< 0.001	31	+22	+2.3	0.007	< 0.001

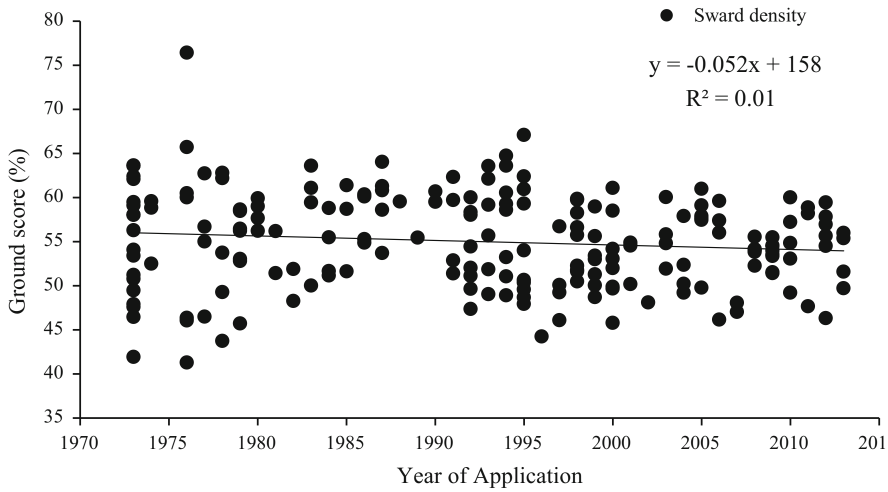

Fig. 3 Genetic gain in sward density of perennial ryegrass varieties under simulated grazing 1973–2013

Table 6 Genetic gain of perennial ryegrass varieties in sward density 1973–2013

	No. of varieties	Gain (%)	Change (GS %)	SE	*p* value
All varieties	197	−3.8	−2.1	0.03	NS
Early	40	−4.9	−2.8	0.07	NS
Intermediate	83	+2.2	+1.2	0.05	NS
Late	74	−7.8	−4.5	0.04	< 0.05
All diploids	115	−1.9	−1.1	0.03	NS
Early diploids	22	−6.3	−3.7	0.07	NS
Intermediate diploids	47	+4.1	+2.3	0.5	NS
Late diploids	46	−4.4	−2.6	0.05	NS
All tetraploids	82	+2.0	+1.1	0.03	NS
Early tetraploids	18	+4.3	+2.2	0.1	NS
Intermediate tetraploids	34	+7.2	+3.5	0.05	NS
Late tetraploids	30	−3.6	−1.9	0.04	NS

was not the actual performance of that variety in any given trial year. It did however remove the year × environment variation between 1973 and 2013 and made all the data from all varieties directly comparable despite most never having been compared in side by side trials.

The DM yield results showed an overall average annual increase in DM yielding potential of 0.52 % under conservation management and 0.35 % under simulated grazing. This was broadly similar to the annual increases reported by other studies such as 0.38 % by Humphreys (1999), 0.4–0.5 % by Easton et al. (2002) and 0.4–0.6 % by Wilkins and Humphreys (2003). These rates of increase are significantly lower than in maize (2.6 %/year; Tollenaar 1989) and typically for cereals (1.0–1.5 %/year; Peltonen-Sainio and Karjalainen 1991; Silvey 1986; Öfversten et al. 2004; Caldenrini et al. 1995). As reported widely and by Wilkins and Humphreys (2003) this is because grain yield improvements were achieved by repartitioning biomass from the shoot into the grain whereas grass yield improvements require total shoot biomass increases. Furthermore, the hybrid vigour boost gained in creating inbred-lines for maize breeding, cant be easily replicated in allogamous grasses.

Although all yields are modified by the G × E factors of the location and are thus site specific, the current study arguably provides a particularly

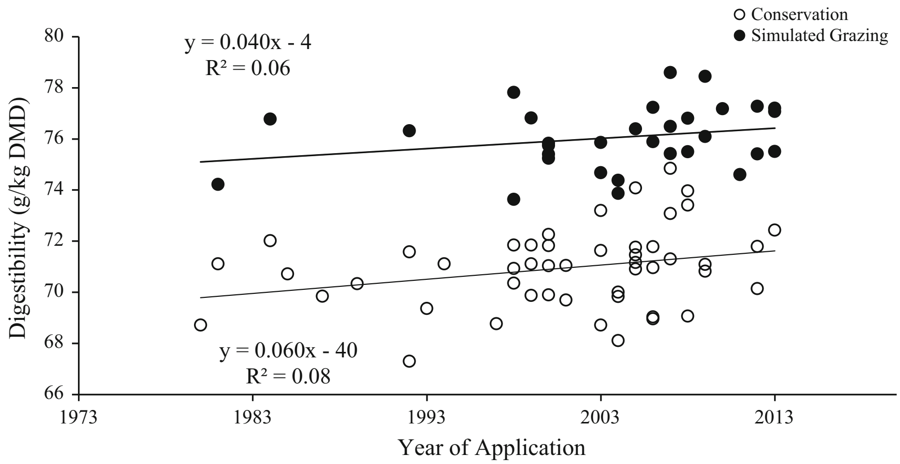

Fig. 4 Genetic gain in digestibility of perennial ryegrass varieties under simulated grazing and conservation managements 1980–2013

Table 7 Genetic gain in dry matter digestibility of perennial ryegrass varieties 1980–2013

	Conservation					Simulated grazing				
	No. of varieties	Gain (%)	Change (g/kg DMD)	SE	*p* value	No. of varieties	Gain (%)	Change (g/kg DMD)	SE	*p* value
All varieties	49	+2.5	+25	0.02	0.07	67	+2.0	+15	0.02	NS
Early	10	+3.2	+22	0.05	NS	13	+1.4	+10	0.03	NS
Intermediate	17	+3.6	+25	0.07	NS	26	+1.4	+10	0.06	NS
Late	22	+1.0	+14	0.04	NS	28	+2.3	+10	0.03	NS
All diploids	23	+1.0	+15	0.02	NS	36	+1.5	+11	0.02	NS
All tetraploids	26	+1.7	+12	0.03	NS	31	+1.6	+12	0.02	NS

definitive measure of the rate of genetic gain in perennial ryegrass, given the use of a single low stress site (low disease levels, mild winters and warm moist summers), under two fixed management regimes for over 40 years. Such a long timeframe is required to make a meaningful measure of genetic progress as breeding new ryegrass varieties is a progressive long term process. During this period, the major technological advancements in plant breeding (Humphreys 2005) and innovations in biology and genetics have helped provide improved perennial ryegrass breeding strategies (Lee et al. 2012). This does not however explain the fluctuating patterns of yield increases observed in the current study.

Although the rapid yield gains observed for the 1990s in both managements were undoubtedly due to the type of selective breeding for superior genetic material described by Connolly (2001), the insight from this 41 year study shows that these periods of high increase rates can equally be regarded as periods of catch up following a lag period within the overall long term trend. The causes of these lag phases are difficult to explain but likely causes are changes in breeding effort and consequences of RL systems. Reduced breeding effort can be caused by a complexity of multifaceted factors. As shown by Gilliland et al. (2007) and Long et al. (2010) changes in farmer preferences, the arrival of a new market leader variety refocusing the efforts of competing breeders away from other areas in a quest to better the new advance or declines in the seed markets. This resulted in a reduction in profitability and in breeding company mergers, all of which reduce the breeding effort either periodically or in specific traits. The objective for variety testers has always been an overall improvement in the agricultural merit of grassland (Camlin 1997), but in a multi-use, multi-harvest crop compromises are made in recommendations. So a variety with excellent conservation yields but below average simulated grazing yields may still be recommended, despite this variety appearing to slow the breeding progress for simulated grazing. This implication may also explain the observation that the spread in performance between varieties did not become more compact as breeders focused on the latest yield improvement.

The fact that the rate of increase was greater for the conservation management than for simulated grazing indicates that varieties can perform differently under each management. These observations provide a strong case against recommending varieties for both conservation and simulated grazing use but for having separate lists for each management, as recently introduced by Meehan and Gilliland (2014). The higher rate of conservation yield improvement may reflect that increasing the very large first or to a lesser degree second silage cut is a simpler breeding objective to achieve an overall yield improvement compared to attempting to increase all the yields across all of the cuts under simulated grazing. More recently this might also reflect breeders selecting different seasonal yield distributions, such as higher spring yields, which was not examined in the current study.

An unexpected observation was that the rates of yield increase within maturity groups were very similar under conservation and surprisingly highest in the early group and lowest in the intermediate group under simulated grazing. The numbers of early variety applications has been substantially lower than for either of the other two maturities for the past 2–3 decades and yet this lower breeding effort has not affected the rate of gain. This may be partly due to a few very high performing recent varieties, but could equally indicate the use of breeding techniques to retard the timing of flowering in early genotypes to facilitate crossing and importing genetic improvements from the intermediate maturing or even the late maturing genotypes. Also somewhat surprising was the greater rate of improvement among the tetraploids compared with the diploids under simulated grazing, whereas both ploidies recorded a relatively similar improvement rate under conservation. A greater rate of gain might have been expected for diploids as they are generally lower yielding than tetraploids indicated by data from the Irish and UK RLs (Connolly 2001), for which the breeding of varieties started much later than for diploids. Equally the greater gain rate of tetraploids over diploids under simulated grazing but not under conservation is not easily understood given that the broad leaved erect and open growth habit of the tetraploids which may possibly make them better adapted to conservation use.

Despite improved persistence being a major focus of breeding programmes (Evans and Williams 1987), there was no significant improvement in sward density since the beginning of the study period. The general trend was of a slow insignificant decline with the late maturity group demonstrating the only significant decline over the 41 years. Given that tetraploids generally have a more open growth habit with a reduced number of tillers per plant, it was notable that this category did achieve positive density gain values, though none were significantly increased. It has been suggested that increased herbage production of grasses may be attributed to increases in tiller density or tiller weight or a combination of both (Nelson and Zarrough 1981; Bircham and Hodgson 1983; Grant et al. 1983; Volenec and Nelson 1983). However, the indication from the current study is that breeders have not sacrificed nor improved sward density significantly to achieve yield gains. With declines in sward density recorded in the current study being largely insignificant, this confirms the findings of Crush et al. (2006); Easton et al. (2011) who found little evidence of recent varieties being any less persistent than older ones.

Overall, it seems very possible that the dominant importance of breeding for improved yield may have had limited impact on sward density and therefore the recommended persistence of newly recommended varieties. With no improvement in variety persistence achieved over the last 40 odd years it must be given careful consideration in plant breeding for the future as pasture persistence remains a trait of high economic value to farmers due to full cultivation and reseeding of pasture being expensive (Wilkins and Humphreys 2003). Although Wilkins (1991) has proposed that selecting for a high ratio of vegetative to reproductive tillers and/or a high rate of appearance of new tillers will improve persistency, without better knowledge of the basic factors regulating tillering, as identified by Parsons and Chapman (2000), Laidlaw (2004), it is unlikely that significant persistence improvements will be achieved while still retaining a stable or increasing biomass yield potential and regrowth capacity.

There was also no evidence of an overall trend for improved digestibility but this may be partly because breeders and testers have only recently begun seeking genetic improvement in grass quality. There was, however a very wide spread of digestibility differences between recommended varieties, which showed that improved varieties had been created, but that much poorer ones were being concurrently recommended. At the upper end of this distribution, it may be due to the development of some specialist varieties such as those with enhanced water soluble carbohydrate content (Wilkins and Humphreys 2003). At the lower end it could equally be due to the RL strategy of seeking overall improvements in varieties across the yield, density and quality parameters. Previously, Posselt (1994) showed that negative correlations exist between DM yield and digestibility, suggesting that selection for higher yielding varieties may be having a negative impact on digestibility, in this study there was no negative association between DM yield increase and quality with digestibility remaining unchanged throughout the duration of the experiment indicating that there is the potential to improve both traits simultaneously.

Similar to the circumstance with improving sward density, the evidence from the current study indicates that the current value given to variety yield increases may need to be reduced in order to reward and promote significant breeding efforts to improve digestibility. In a similar study undertaken by Sampoux et al. (2011) over 40 years, gains in DM yield achieved in diploid perennial ryegrass varieties released on European National lists were assessed and it was shown that significant gains in all three primary production traits DM yield, persistency and quality can be achieved simultaneously. This study was comparing gains in 21 registered varieties bred for National lists compared to seven natural populations collected in natural meadows. In the current study, varieties were bred from a concentrated pool of genetic material selected and crossed year on year and tested through a rigorous evaluation programme to achieve genetic gain. Variations in genetic material between the two studies coupled with variation in the size of both data sets makes it difficult to compare gains achieved across the three production traits.

Ultimately, increased DM production is the key trait in plant production which drives the productivity and sustainability of pasture-based farming systems. While overall DM yield gain is significant across varieties registered on RLs over the past 40 years, gains in DM production in pasture deficit periods such as spring and autumn may well be viewed of higher economic value by farmers for commercial use especially as pasture performance comes under increased pressure due to limitations in land availability and environmental constraints in the future (Parsons et al. 2011), Sampoux et al. (2011) identified over 40 years, gains in DM yield of perennial ryegrass varieties released on European National lists were primarily in the summer and autumn but no gain was achieved in spring DM yield production where pasture supplementation requirements are at their highest. Gain in DM yield may very well need to be assessed on such pasture growth deficit periods in the year to ensure farmers are reaping maximum economic benefit from newly bred recommended varieties.

Nonetheless, a continuation of the yield gains found in the current study plus application of new efforts towards similar gains in seasonal DM production, sward density and nutritional quality are key factors in reducing the carbon footprint and greenhouse gas emissions while increasing the feed efficiency of the ruminant sector. The evidence from the current study shows how a regional RL has been a valuable tool over many years in aiding government to achieve improvements in these key policy areas.

Conclusion

In overall conclusion, this study has shown that perennial ryegrass breeders have achieved significant increases in DM yield production over time and at credible annual rates in comparison to grain crops, given the greater challenge of increasing the total shoot biomass in an allogamous species. These increases were evident in all ploidy and maturity sub-groups under both conservation and simulated grazing managements. There was no evidence of sward density improving despite large gains in DM yield. This indicates that breeders have improved yield capacity of perennial ryegrass plants without sacrificing sward density significantly. However, sward density was in a slight decline so may need to be considered in the future as a loss in persistency performance could be a retrograde step for plant breeding and have a negative impact on economic performance of newly bred recommended varieties on farm. There was almost no evidence of any improvements in digestibility under either management regime but the very wide variation in grass quality between contemporary varieties indicated that improvements are possible. Given that the recognition of digestibility improvement was only relatively recently introduced to the testing system, further advances need to be realised. This conclusion recognises that the variety testing system is an important catalyst driving the pace and influencing the direction of advances made by plant breeders. For this reason great care is required when deciding how different performance parameters are used in the listing decisions of new varieties as this can promote important improvements such as better grass quality in the future but equally cause significant effects such as the potential impact on sward density and persistence.

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